

SUBTRIBAL CLASSIFICATION OF THE NEW WORLD ERAGROSTIDEAE (POACEAE: CHLORIDOIDEAE)

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ABSTRACT

A subtribal classification system for 38 genera of Eragrostideae that occur in the New World is presented. Seven recognized subtribes include: Eleusininae, Eragrostidinae, Monanthochloinae, Muhlenbergiinae, Munroinae, Sporobolinae, and Uniolinae. A comparative discussion outlining the recent classification history is included. Diagnostic fully comparative descriptions are given for each subtribe and a new subtribe, Munroinae, is validated.

RESUMEN

Se presenta un sistema de clasificación tribal de 38 géneros de Eragrostideae que viven en el Nuevo Mundo. Las siete subtribus reconocidas son: Eleusininae, Eragrostidinae, Monanthochloinae, Muhlenbergiinae, Munroinae, Sporobolinae, y Uniolinae. Se incluye una discusión comparativa que esboza la historia de la clasificación reciente. Se ofrece una descripción diagnóstica comparativa completa de cada subtribu y se valida una nueva subtribu, Munroinae.

INTRODUCTION

The tribe Eragrostideae in the subfamily Chloridoideae includes approximately 80 genera and 1000 species or about one-tenth of all grasses. These

taxa are primarily distributed in the subtropical to tropical regions in arid climates with centers of distribution in the savannahs of southern Africa and north central Mexico. In the New World or Western Hemisphere, we recognize 38 genera and about 427 species with the highest concentration in north central Mexico and southwestern United States.

Within the Eragrostideae there is considerable variation in morphology, anatomy, and cytology (Peterson 1988, 1989; Peterson & Annable 1990, 1991, 1992; Peterson et al. 1989, 1993, 1996; Peterson & Herrera 1995; Valdes-Reyna & Hatch 1991). It is difficult, if not impossible to select diagnostic characteristics that exclusively delimit the Eragrostideae from other tribes in the Chloridoideae. However, the tribe commonly has paniculate inflorescences (occasionally racemose), laterally compressed or terete (rarely dorsiventral) spikelets, lemmas 3-nerved (occasionally 1 or more than 3-nerved), and disarticulation typically above the glumes (Peterson et al. 1996).

In *Flora Capensis*, Stapf (1898) first used the tribal name Eragrosteae (= Eragrostideae) where he recognized four genera: *Desmostachya* (Hook. f) Stapf, *Diplachne* P. Beauv. (= *Leptochloa*), *Eragrostis*, and *Pogonarthria* Stapf. Pilger (1956) increased the number of taxa in the Eragrostideae to include 53 genera in six subtribes. Five out of the six Eragrostideae subtribes (Eragrostinae, Lycurinae, Muhlenbergiinae, Scleropogoninae, and Sporobolinae) used by Pilger contain indigenous New World genera.

Relationships among these genera have been problematic and agrostologists have attempted to sort out a classification that reflects common ancestry. The primary objective of the present study is to present a comprehensive, fully comparative classification system for the 38 native and introduced New World genera of the Eragrostideae. In addition to presenting our new classification, we include a review of the major classifications used in the last half century. A proposed classification recognizing seven subtribes is given to elucidate probable phylogentic relationships among the New World genera.

METHODS

A discussion is presented for those classification treatments that were considered important for the New World genera of the Eragrostideae and these include: Hitchcock and Chase (1951), Pilger (1954, 1956), Gould and Shaw (1983), Clayton and Renvoize (1986), and Watson and Dallwitz (1992). An outline of these classifications is presented in Table 1. Associated with Table 1 is a discussion on the characters used by the authors to delimit the categories. This information was extracted from their keys and descriptions. Within each classification outline we primarily included only those categories pertinent to the New World genera. Recognition of

subtribes was based on a synthesis of data from relevant systematic disciplines and includes morphological, anatomical, cytological, ecological, and molecular characteristics. In addition, this classification reflects our knowledge gained from experience studying these taxa in the laboratory and field.

The DELTA system (Dallwitz 1980; Dallwitz et al. 1993) was used in the selection of characters and production of diagnostic comparative descriptions of the seven recognized subtribes. Initially, a list of 90 characters was constructed to account for variation at the generic level for the Eragrostideae. A full range and adequate number of herbarium specimens were analyzed and data were recorded for the 38 recognized New World genera. A comprehensive taxonomic account for these genera is forthcoming (Peterson et al. 1996). INTKEY was used to combine data for the genera of a subtribe. For example, the DELTA format data of the Monanthochloinae was produced through INTKEY by combining the data for the members, specifically *Allolepis*, *Distichlis*, *Jouvea*, *Monanthochloë*, *Reederochloa*, and *Swallenia*. This combined DELTA format data was converted to the natural language description presented here. Selection of the 21 characters presented in these descriptions was based on their diagnostic value and on the value of the character in distinguishing among the subtribes. Additional methods concerning the application of the DELTA programs can be found in Webster (1988, 1992a, 1992b).

HISTORICAL CLASSIFICATION

It is important to present a discussion of the relevant classifications of this group. Included here in chronological order are discussions of the treatments by Hitchcock and Chase (1951), Pilger (1954, 1965), Gould and Shaw (1983), Clayton and Renvoize (1986), and Watson and Dallwitz (1992). Important characteristics used to distinguish among their categories are outlined together with the placement of our 38 New World genera.

The Eragrostideae are treated by Hitchcock and Chase (1951) in three tribes: Agrostideae, Chlorideae, and Festuceae (Table 1). Their Agrostideae (*Blepharoneuron*, *Calamovilfa*, *Crypsis*, *Lycurus*, *Muhlenbergia*, *Sporobolus*) is based on the presence of perfect, 1-flowered spikelets, and paniculate inflorescences. Although the number of florets per spikelet is a very diagnostic generic characteristic, its use to determine tribal and subfamily relationships has proven fallacious. Therefore, members of their Agrostideae have been subsequently re-aligned to other tribes in the Poaceae. Their Chlorideae included six genera (*Dactyloctenium*, *Eleusine*, *Leptochloa*, *Munroa*, *Trichoneura*, *Tripogon*) are characterized as having 1-to several-flowered spikelets in two rows along one side of a continuous rachis. The inflorescence consists of spikes or spike-like racemes, either solitary, digitate, or racemosely arranged along the main axis. The Festuceae as interpreted by Hitchcock and Chase

(1951) includes the following genera: *Blepharidachne*, *Distichlis*, *Eragrostis*, *Eragrostis* (in part, *Neeragrostis*), *Monanthochloë*, *Redfieldia*, *Scleropogon*, *Ectosperma* (= *Swallenia*), *Neyraudia*, *Tridens* (in part, *Dasyochloa*, *Erioneuron*), *Triplasis*, *Uniola*, *Vaseyochloa*. Nine genera (*Allolepis*, *Bealia*, *Chaboissaea*, *Gouinia*, *Jouvea*, *Neesiochloa*, *Pereilema*, *Sohnsia*, *Steirachne*, *Reederochloa*, *Tetrachne*) were not treated by Hitchcock and Chase (1951) since they do not occur in the United States.

A progressive classification of the grass family was given by Pilger (1954, 1956) who placed our 38 genera into five different tribes in two different subfamilies (Table 1). It is worthy to note that he states exceptions to most if not all characters used to define his categories. The following characteristics were used to differentiate the Eragrosteae from the other five tribes in subfamily Eragrostoideae: spikelets in loose or contracted panicles (often compounded in racemes or spikes); branches spirally inserted; glumes usually shorter than the lemma; upper floret in many-flowered spikelets often sterile; lemma usually 1 or 3-nerved, membranous to leathery; lemma apex entire, crenate, toothed or lobed, if aristate, the awn arising from the mid-nerve; lemma nerves often hairy; stamens 2–3; fruits usually loosely surrounded by the palea (often becoming free); pericarp thin (often loosening and leaving the seeds naked); hilum small and basal; base chromosome number 8 or 10.

Pilger's Eragrosteae included six subtribes (Eragrostinae, Scleropogoninae, Lycurinae, Garnotiinae, Sporobolinae, and Muhlenbergiinae). The Eragrostinae (including *Blepharidachne*, *Dactyloctenium*, *Eleusine*, *Eragrostis*, *Leptochloa*, *Munroa*, *Neesiochloa*, *Neyraudia*, *Redfieldia*, *Steirachne*, *Trichoneura*, *Tridens*, *Triplasis*, *Tripogon*) was separated by multi-flowered spikelets with perfect florets. The Scleropogoninae with only *Scleropogon* was characterized by unisexual spikelets with the female spikelets long aristate. Pilger's Lycurinae (including *Lycurus*) was characterized by glumes finely aristate and single-flowered spikelets. The Sporobolinae which includes *Blepharoneuron*, *Crypsis*, and *Sporobolus*, was differentiated by single-flowered spikelets, thin glumes, aristate lemmas, and rounded fruits. The Muhlenbergiinae (including *Muhlenbergia*) was separated by glumes shorter than the lemma, single-flowered spikelets, and narrow cylindrical caryopses. Pilger's final tribe that includes New World genera, the Jouveae (*Jouvea*), was characterized by dimorphic, unisexual spikelets, with or without a rachilla extension (in female spikelets), 1-flowered female spikelets, rudimentary glumes, inflorescence a spike with few spikelets, and a thick, grooved rachis.

Pilger (1954) placed eight of our genera in the subfamily Festucoideae in three tribes (Festuceae, Aveneae, Arundineae, see Table 1). The Festuceae was separated by paniculate inflorescences, spikelets 1 to many-flowered,

glumes shorter than the florets, and lemmas 3 to 5-nerved. His treatment included six of our 38 genera in three subtribes: Monanthochloinae, Festucinae, and Melicinae. The Monanthochloinae (including *Monanthochloë*) was characterized by spikelets without "outer" glumes, unisexual spikelets (dioecious or monocious), and short stiff leaves. The Festucinae (including *Distichlis*, *Uniola*, *Tetrachne*) was defined by spikelets with two outer glumes, lemmas 5 to several-nerved (rarely 3-nerved), and the lemma apex entire or bidentate. The Melicinae (including *Ectosperma* and *Vaseyochloa*) was distinguished by a several to many-nerved lemma, a paniculate inflorescence, and lemmas blunt and rounded on the back. *Calamovilfa* was placed in the Aveneae, a tribe characterized by disarticulation above the glumes, relatively long glumes, and mostly 5-nerved lemmas. The Arundineae (including *Gouinia*) was described as mostly tall reed-like in habit, rachilla or lemma hairy, outer glume shorter or equalling the spikelet length, 3 or 5-nerved lemmas, and lemmas with a straight or twisted awn. New World genera not treated by Pilger included *Allolepis*, *Reederchloa*, and *Sohnsia*.

The classification presented in Gould and Shaw (1983) represents a significant advance over that given by Hitchcock and Chase (1951). This advancement was the result of Gould's (1968, 1983) synthesis of the advancements from 1950 to 1983 (eg. Stebbins & Crampton 1961) in agrostology, specifically in the areas of anatomy, cytology, ecology, and morphology. Gould and Shaw (1983) divided the Chloridoideae into eight tribes, whereas Hitchcock and Chase only include four tribes with chloridoid genera (Agrostideae, Chlorideae, Festuceae, Zoysieae).

Five tribes recognized by Gould and Shaw (1983) do not include genera that we place in the Eragrostideae. Each of these five possess diagnostic characters that separate them from the genera of the Eragrostideae. A key to the tribes is not given by Gould and Shaw; however, diagnostic characters can be extracted from the brief descriptions associated with each tribe. The Pappophoreae is best distinguished by the presence of lemmas with 9 or more nerves and awns. Secondary characters include a paniculate inflorescence with 3 to several florets per spikelet, ligule a line of hairs, and point of disarticulation close to the glumes. The Chlorideae is distinguished by an inflorescence of "a unilateral spike or of few to several unilateral spicate primary branches." Secondary diagnostic characters are spikelets with a single fertile floret and one or more reduced florets, 3-nerved lemmas, and ligule a line of hairs. The Orcuttieae is distinguished by the absence of a ligule and the undifferentiated leaf blade and sheath. Additional characters include persistent spikelets, 5-nerved lemmas, and paniculate inflorescences with several-flowered spikelets. Gould and Shaw define the Aristideae by 1-flowered spikelets, disarticulation above the glumes, and lemmas with an awn column usually bearing 3 awns. In addition they give

many anatomical characters, such as: dumbbell-shaped silica cells, two parenchyma sheaths, and elongate chlorenchyma cells. The last tribe lacking genera we place in the Eragrostideae, Zoysieae, is differentiated by a ligule as a line of hairs, inflorescence a contracted raceme of 1-flowered spikelets, and disarticulation at the base of the spikelet.

As Table 1 indicates, Gould and Shaw (1983) place our New World Eragrostideae genera in three tribes (Aeluropodeae, Eragrosteae, Uniioleae), with some not treated. The Uniioleae, including only *Uniola* in the U. S., was distinguished by disarticulation below the glumes, ligule a line of hairs, large paniculate inflorescences, and several to many-flowered spikelets that have the lowermost and uppermost florets sterile. Additional anatomical characters include a leaf epidermis with club-shaped bicellular microhairs and square or saddle-shaped silica cells. Their concept of the Aeluropodeae included four of our New World genera (*Allolepis*, *Distichlis*, *Monanthochloë*, *Swallenia*). Their tribe was differentiated by the presence of a stoloniferous or rhizomatous habit, usually occurring in saline habitats, short pungent leaf blades, and inflorescences a contracted panicle or raceme, usually unisexual. Excluding those genera not treated by Gould and Shaw, the remaining 22 New World genera were lumped into the Eragrosteae. This tribe is poorly defined with numerous exceptions to all characters used to recognize the group. However, important characters include a 3-nerved lemma, 1-several flowered spikelets, a paniculate inflorescence with some rebranching of the primary branches, and disarticulation mostly above the glumes. New World genera not treated by Gould and Shaw (1983) include *Bealia*, *Chaboissaea*, *Gouinia*, *Jouvea*, *Neesiochloa*, *Neyraudia*, *Pereilema*, *Reederochloa*, *Sohnsia*, *Steirachne*, and *Tetrachne*. All of which occur in regions south of the United States.

Clayton and Renvoize (1986) separate the Chloridoideae into five tribes (Pappophoreae, Orcuttieae, Eragrostideae, Leptureae, and Cynodonteae) and nine subtribes; with five subtribes in the Eragrostideae and four subtribes in the Cynodonteae. Our New World genera of the Eragrostideae are all placed in their concept of the Eragrostideae. The Pappophoreae includes five genera and is distinguished by a many-nerved, lobed, and awned lemma, a narrow paniculate inflorescence, spikelets with several florets (commonly with the lower 2 or more florets bisexual), and disarticulation above the glumes. The Orcuttieae is delimited on leaves that are scarcely differentiated into a blade and sheath, absence of a ligule, viscid and aromatic leaf blades, lemmas with 13–15 nerves, and absence of lodicules. The Leptureae, consisting of *Lepturus*, is separated from other members of the subfamily by having a single cylindrical bilateral raceme with the spikelets alike, borne edgewise on and embedded in hollows in the fragile rachis. There do not appear to be any New World chloridoids that are morphologically similar

TABLE 1. Tribal classifications of the Chloridoideae.

Hitchcock & Chase (1951)
Subfamily Festucoideae
1. Agrostideae = <i>Blepharoneuron</i> , <i>Calamovilfa</i> , <i>Crypsis</i> , <i>Lycurus</i> , <i>Muhlenbergia</i> , <i>Sporobolus</i>
2. Aveneae
3. Bambuseae
4. Chlorideae = <i>Dactyloctenium</i> , <i>Eleusine</i> , <i>Leptochloa</i> , <i>Munroa</i> , <i>Trichoneura</i> , <i>Tripogon</i>
5. Festuceae = <i>Blepharidachne</i> , <i>Distichlis</i> , <i>Eragrostis</i> (including <i>Neeragrostis</i>), <i>Monanthochloë</i> , <i>Redfieldia</i> , <i>Scleropogon</i> , <i>Ectosperma</i> (= <i>Swallenia</i>), <i>Neyraudia</i> , <i>Tridens</i> (in part, <i>Dasyochloa</i> , <i>Erioneuron</i>), <i>Triplasis</i> , <i>Uniola</i> , <i>Vaseyochloa</i>
6. Hordeae
7. Oryzeae
8. Phalarideae
9. Zizanieae
10. Zoysieae
Not Treated = <i>Allolepis</i> , <i>Bealia</i> , <i>Chaboissaea</i> , <i>Gouinia</i> , <i>Jouvea</i> , <i>Neesiochloa</i> , <i>Pereilema</i> , <i>Sohnsia</i> , <i>Steirachne</i> , <i>Reederochloa</i> , <i>Tetrachne</i>

Pilger (1954, 1956)
Subfamily Eragrostoidae
1. Eragrosteae
a. Eragrostinae = <i>Blepharidachne</i> , <i>Dactyloctenium</i> , <i>Eleusine</i> , <i>Eragrostis</i> (including <i>Neeragrostis</i>), <i>Leptochloa</i> , <i>Munroa</i> , <i>Neesiochloa</i> , <i>Neyraudia</i> , <i>Redfieldia</i> , <i>Steirachne</i> , <i>Trichoneura</i> , <i>Tridens</i> (includes <i>Dasyochloa</i> and <i>Erioneuron</i>), <i>Triplasis</i> , <i>Tripogon</i>
b. Scleropogoninae = <i>Scleropogon</i>
c. Lycurinae = <i>Lycurus</i> , <i>Pereilema</i>
d. Garnotiinae
e. Sporobolinae = <i>Blepharoneuron</i> , <i>Crypsis</i> , <i>Epicampes</i> (= <i>Muhlenbergia</i> in part), <i>Sporobolus</i>
f. Muhlenbergiinae = <i>Muhlenbergia</i> (including <i>Bealia</i> and <i>Chaboissaea</i>)
2. Phaenospermeae
3. Chlorideae
a. Lepturinae
b. Chloridinae
4. Aristideae
5. Lappagineae
6. Jouveeae = <i>Jouvea</i>

Subfamily Festucoideae
1. Festuceae
a. Monanthochloinae = <i>Monanthochloë</i>
b. Festucinae = <i>Distichlis</i> , <i>Uniola</i> , <i>Tetrachne</i>
c. Melicinae = <i>Ectosperma</i> (= <i>Swallenia</i>), <i>Vaseyochloa</i>
2. Aveneae = <i>Calamovilfa</i>
3. Arundineae = <i>Gouinia</i>

Not Treated = *Allolepis*, *Reederochloa*, *Sohnsia*

Gould & Shaw (1983)
1. Eragrosteae = <i>Blepharidachne</i> , <i>Blepharoneuron</i> , <i>Calamovilfa</i> , <i>Crypsis</i> , <i>Dactyloctenium</i> , <i>Eleusine</i> , <i>Eragrostis</i> , <i>Erioneuron</i> (including <i>Dasyochloa</i>), <i>Leptochloa</i> , <i>Lycurus</i> , <i>Muhlenbergia</i> , <i>Munroa</i> , <i>Neeragrostis</i> , <i>Redfieldia</i> , <i>Scleropogon</i> , <i>Sporobolus</i> , <i>Trichoneura</i> , <i>Tridens</i> , <i>Triplasis</i> , <i>Tripogon</i> , <i>Vaseyochloa</i>
2. Aeluropodeae = <i>Allolepis</i> , <i>Distichlis</i> , <i>Monanthochloë</i> , <i>Swallenia</i>
3. Unioleae = <i>Uniola</i>

TABLE 1. (Continued)

4. Pappophoreae
5. Chlorideae
6. Orcuttieae
7. Aristideae
8. Zoysieae
Not Treated = <i>Bealia</i> , <i>Chaboissaea</i> , <i>Gouinia</i> , <i>Jouvea</i> , <i>Neesiochloa</i> , <i>Neyraudia</i> , <i>Pereilema</i> , <i>Reederochloa</i> , <i>Sohnsia</i> , <i>Steirachne</i> , <i>Tetrachne</i>
Clayton & Renvoize (1986)
1. Pappophoreae
2. Orcuttieae
3. Eragrostideae
b. Scleropogoninae = <i>Scleropogon</i>
a. Triodiinae
b. Uniolinae = <i>Tetrachne</i> , <i>Uniola</i>
c. Monanthochloinae = <i>Allolepis</i> , <i>Distichlis</i> , <i>Jouvea</i> , <i>Monanthochloë</i> , <i>Reederochloa</i> , <i>Swallenia</i>
d. Eleusininae = <i>Blepharidachne</i> , <i>Blepharoneuron</i> , <i>Dactyloctenium</i> , <i>Eleusine</i> , <i>Eragrostis</i> (including <i>Neeragrostis</i>), <i>Erioneuron</i> (including <i>Dasyochloa</i>), <i>Gouinia</i> , <i>Leptochloa</i> , <i>Munroa</i> , <i>Neesiochloa</i> , <i>Neyraudia</i> , <i>Redfieldia</i> , <i>Scleropogon</i> , <i>Sohnsia</i> , <i>Steirachne</i> , <i>Trichoneura</i> , <i>Tridens</i> , <i>Triplasis</i> , <i>Tripogon</i> , <i>Vaseyochloa</i>
e. Sporobolinae = <i>Calamovilfa</i> , <i>Crypsis</i> , <i>Lycurus</i> , <i>Muhlenbergia</i> (including <i>Bealia</i> and <i>Chaboissaea</i>), <i>Pereilema</i> , <i>Sporobolus</i>
4. Leptureae
5. Cynodonteae
a. Pommereullinae
b. Chloridinae
c. Boutelouinae
d. Zoysiinae
Watson & Dallwitz (1992)
1. Triodieae
2. Pappophoreae
3. Orcuttieae
4. Chlorideae = <i>Allolepis</i> , <i>Bealia</i> , <i>Blepharidachne</i> , <i>Blepharoneuron</i> , <i>Calamovilfa</i> , <i>Chaboissaea</i> , <i>Crypsis</i> , <i>Dactyloctenium</i> , <i>Dasyochloa</i> , <i>Distichlis</i> , <i>Eleusine</i> , <i>Eragrostis</i> , <i>Erioneuron</i> , <i>Gouinia</i> , <i>Jouvea</i> , <i>Leptochloa</i> , <i>Lycurus</i> , <i>Monanthochloë</i> , <i>Muhlenbergia</i> , <i>Munroa</i> , <i>Neeragrostis</i> , <i>Neesiochloa</i> , <i>Neyraudia</i> , <i>Pereilema</i> , <i>Redfieldia</i> , <i>Reederochloa</i> , <i>Scleropogon</i> , <i>Sohnsia</i> , <i>Sporobolus</i> , <i>Steirachne</i> , <i>Swallenia</i> , <i>Tetrachne</i> , <i>Trichoneura</i> , <i>Tridens</i> , <i>Triplasis</i> , <i>Tripogon</i> , <i>Uniola</i> , <i>Vaseyochloa</i>

to *Lepturus*. Clayton and Renvoize (1986) characterize the Cynodonteae, which includes the subtribes Chloridinae and Boutelouinae, as having tough unilateral racemes (these single digitate or scattered along the axis), spikelets with one fertile floret (with or without additional staminate or sterile florets), 1–3(–5)-nerved glumes, nerveless or 3-nerved lemmas, and fruit occasionally with a free pericarp. Some genera of the Chloridinae are morphologically similar to members of our Eragrostideae. Specific examples include: *Eustachys*, *Chloris*, and *Cynodon* with 2-many digitate racemes;

Microchloa with a single raceme bearing spikelets on a semiterete rachis; and *Schedonnardus* with several racemes on a single axis bearing distant appressed spikelets on a three-angled rachis.

As indicated in Table 1, Clayton and Renvoize (1986) separate the Eragrostideae into five subtribes (Triodiinae, Uniolinae, Monanthochloinae, Eleusininae, and Sporobolinae). The Triodiinae includes only Australian genera and is best distinguished by highly xeromorphic pungent and needle-like leaf blades and disarticulation below each floret. The leaves have greatly reduced chlorenchyma tissue that occurs as narrow tracts along the stomatal grooves. The Uniolinae included the New World genera *Tetrachne* and *Uniola* and is diagnosed by the presence of several to many fertile florets, disarticulation below the glumes, and glumes shorter than the strongly keeled lemmas. Clayton and Renvoize's third subtribe the Monanthochloinae includes the New World genera *Allolepis*, *Distichlis*, *Jouvea*, *Monanthochloë*, *Reederchloa*, and *Swallenia*. Significant diagnostic characters of this group include are distichous often pungent leaf blades, spikelets with several to many perfect florets, disarticulation usually below each floret, and lemmas 5–13-nerved and thick textured. The Sporobolinae included six New World genera (*Calamovilfa*, *Crypsis*, *Lycurus*, *Muhlenbergia*, *Pereilema*, *Sporobolus*). Their concept of *Muhlenbergia* included *Bealia* and *Chaboissaea*. Important characters for this subtribe included inflorescence a panicle, spikelets 1-flowered, the rachilla not extending above the floret, and lemma 1–3-nerved, usually membranous. Clayton and Renvoize's (1986) Eleusininae includes 20 New World genera: *Blepharidachne*, *Blepharoneuron*, *Dactyloctenium*, *Eleusine*, *Eragrostis* (including *Neeragrostis*), *Erioneuron* (including *Dasyochloa*), *Gouinia*, *Leptochloa*, *Munroa*, *Neesiochloa*, *Neyraudia*, *Redfieldia*, *Scleropogon*, *Sohnsia*, *Steirachne*, *Trichoneura*, *Tridens*, *Triplasis*, *Tripogon*, *Vaseyochloa*. Important characters in this diverse subtribe include: spikelets with 2-many fertile florets, lemmas 3-nerved, and an inflorescence more often a raceme but sometimes a panicle.

Watson and Dallwitz (1992) recognized four tribes within subfamily Chloridoideae. These include the Triodieae, Pappophoreae, Orcuttieae, and Chlorideae. The distinguishing characters among these tribes are not clearly defined in their database nor hardcopy publication. However, in the interactive database, genera of the Orcuttieae can be separated from the Chlorideae by not having leaves that are clearly differentiated into a sheath and blade. Genera of the Pappophoreae can be characterized by lemmas with 7-many nerves and 7-many lobes, disarticulation above the glumes, paniculate inflorescences, and relatively long glumes. New World Troidieae (including only *Triodia*) can be differentiated from other chloridoids by indurate lemmas and hard, needle-like leaf blades. All of our New World

Eragrostideae are grouped by Watson and Dallwitz (1992) in the Chlorideae without recognition of subtribal categories.

PROPOSED CLASSIFICATION

Based primarily on morphological characteristics, we have attempted to place the genera of Eragrostideae into natural groups. We have included the naturalized genera along with the autochthonous genera, even though many of the remaining genera in each of the subtribes may be centered in other continents. By using results from our phenetic analysis (Peterson et al. 1996) and review of the literature, especially on data from chloroplast DNA restriction site comparisons (Duvall et al. 1994), the New World Eragrostideae is appropriately divided into seven subtribes: Eleusininae, Eragrostidinae, Monanthochloinae, Muhlenbergiinae, Munroinae, Sporobolinae, and Uniolinae (see Table 2).

Dactyloctenium and *Eleusine* are the New World representatives of the Eleusininae. An inflorescence with digitate primary branches is the diagnostic characteristic for this subtribe. Additional significant characters that define the Eleusininae include the presence of a free pericarp and a membranous ligule. The Eleusininae obviously has arisen in the Old World tropics, quite possibly in East Africa where species diversity of *Dactyloctenium* and *Eleusine* is greatest. The few species represented in the New World of these two genera suggest migration from the Old World has occurred recently.

The Eragrostidinae is, at best, an unnatural grouping of convenience, since the relationships among these 15 genera is poorly understood (Table 2). However, based on the full range of characters used here, these genera are presently excluded from our other subtribes. More than one floret per spikelet, fruit with an adnate pericarp, and base chromosome number of 10, 20 or 30 distinguishes the Eragrostidinae from the Eleusininae, Munroinae, Sporobolinae, and the Uniolinae. Important characters that can be used to separate the Eragrostidinae from most of the Monanthochloinae and Muhlenbergiinae include leaf arrangement (distichous in Monanthochloinae), sexuality (dioecious in Monanthochloinae, except *Swallenia*), lemma texture (relatively thick in Monanthochloinae), and number of lemmatal nerves (3-nerved in Muhlenbergiinae). No characters exclusively distinguish the Eragrostidinae from the Muhlenbergiinae. Eventually, as new data becomes available we suspect that many of these 15 taxa will be aligned within other current subtribes or placed within new, smaller monophyletic assemblages.

The Uniolinae is a curious small subtribe that includes only four genera worldwide (Clayton & Renvoize 1986), three distributed in Africa and *Uniola* centered along the subtropical and tropical coastal regions of North

TABLE 2. The subtribal classification of the New World Eragrostideae.

Eleusininae Dumort., Anal. Fam. 63. 1829. TYPE: <i>Eleusine</i>	
Genera:	
<i>Dactyloctenium</i>	<i>Eleusine</i>
Eragrostidinae Presl, Rel. Haenk., 1:273. 1830. TYPE: <i>Eragrostis</i>	
Genera:	
<i>Eragrostis</i>	<i>Sobnsia</i>
<i>Gouinia</i>	<i>Steirachne</i>
<i>Leptochloa</i>	<i>Trichoneura</i>
<i>Neeragrostis</i>	<i>Tridens</i>
<i>Neesiochloa</i>	<i>Triplasis</i>
<i>Neyraudia</i>	<i>Tripogon</i>
<i>Redfieldia</i>	<i>Vaseyochloa</i>
<i>Scleropogon</i>	
Monanthochloinae Potztal, Willdenowia 5:472. 1969. TYPE: <i>Monanthochloë</i>	
Genera:	
<i>Allolepis</i>	<i>Monanthochloë</i>
<i>Distichlis</i>	<i>Reederochloa</i>
<i>Jouvea</i>	<i>Swallenia</i>
Muhlenbergiinae Pilger, Nat. Pfl. Fam. ed.2, 14d:168. 1956. TYPE: <i>Muhlenbergia</i>	
Genera:	
<i>Bealia</i>	<i>Lycurus</i>
<i>Blepharoneuron</i>	<i>Muhlenbergia</i>
<i>Chaboissaea</i>	<i>Pereilema</i>
Munroinae Parodi ex P. M. Peterson, Gram. Bonar. ed. 4:28. 1946, nom nud. TYPE: <i>Munroa</i>	
Genera:	
<i>Blepharidachne</i>	<i>Erioneuron</i>
<i>Dasyochloa</i>	<i>Munroa</i>
Sporobolinae Benth., J. Linn. Soc., Bot. 19:30. 1881. TYPE: <i>Sporobolus</i>	
Genera:	
<i>Calamovilfa</i>	<i>Sporobolus</i>
<i>Crypsis</i>	
Uniolinae Clayton, Kew Bull. 37:417. 1982. TYPE: <i>Uniola</i>	
Genera:	
<i>Tetrachne</i>	<i>Uniola</i>

and Central America. Presence of 5–20 florets per spikelet, fruit with a free pericarp, and ligule a line of hairs are characters, when used in combination, that serve to distinguish the Uniolinae from the other subtribes. Characters of secondary significance include: a 3–9-nerved lemma, primary inflorescence branches racemose or paniculate, and lemma entire at the apex. The Uniolinae shows some affinities with the Eleusininae, since both subtribes contain species with free pericarps, laterally flattened spikelets, and spikelets that are two-ranked along primary inflorescence branches.

Calamovilfa, *Crypsis*, and *Sporobolus* are the New World members of the Sporobolinae, which is exclusively defined by the presence of a 1-nerved lemma. Secondary diagnostic characters include one floret per spikelet and a line of hairs for a ligule. The Sporobolinae are closely linked to the Eleusininae and Uniolinae, as all three subtribes possess fruits with free pericarps. Our analysis does not indicate a close affinity between the Muhlenbergiinae and the Sporobolinae even though both have a one-flowered spikelet. Origin of the Sporobolinae probably lies in Africa or the Eastern Mediterranean where species diversity is greatest.

Allolepis, *Distichlis*, *Jouvea*, *Monanthochloë*, *Reederochloa*, and *Swallenia* are the New World members of the Monanthochloinae (Table 2). For most taxa, the presence of distichous leaf arrangement, thick textured lemmas, and the dioecious habit distinguishes this subtribe. Secondary diagnostic characters include florets 2–25 per spikelet, fruit with an adnate pericarp, and lemmas entire at the apex. Numerous morphological and anatomical adaptations, i.e., distinctly distichous leaf arrangement and bicellular microhairs with enlarged bases, are found in some members of this subtribe. These adaptations are in direct response to the environment, since most of the species occur in saline habitats. Based on our phenetic analyses and those by Soderstrom and Decker (1963, 1964, 1965), the Monanthochloinae seems to be a good monophyletic unit. The Monanthochloinae is primarily New World in distribution, only *Aeluropus* Trin. is restricted to the Mediterranean, northern China, Ethiopia, and Sri Lanka.

The distribution of the Muhlenbergiinae is almost entirely New World, only approximately eight of the 160 species of *Muhlenbergia* are known to occur in southern Asia. The six genera of the Muhlenbergiinae (*Bealia*, *Blepharoneuron*, *Chaboissaea*, *Lycurus*, *Muhlenbergia*, *Pereilema*) are characterized by 1–3 florets per spikelet, 3-nerved lemmas, true caryopses, and a base chromosome number of 8 or 10. These characters do not adequately distinguish the Muhlenbergiinae from the Munroinae. However, the Munroinae always has 2–12 florets per spikelet and the lemma apex is usually emarginate to cleft, whereas, the Muhlenbergiinae usually has a single floret per spikelet and the lemma apex is mostly entire. Evidence from molecular data supports this subtribe as being monophyletic (Duvall et al. 1994).

The Munroinae, originally named by Parodi, is formally described below. At present, this subtribe consists exclusively of the following New World genera: *Blepharidachne*, *Dasyochloa*, *Erioneuron*, and *Munroa*. Diagnostic characteristics of the subtribe include lemmas with emarginate to cleft apices and a base chromosome number of $x = 7$ or 8. Molecular studies support the conclusion that the Munroinae evolved from a common ancestor (Duvall et al. 1994).

Munroinae Parodi ex P. M. Peterson, subtribus nov. Parodi, Gram. Bonar. ed. 4:28. 1946, nom nud.

Vaginae ciliatae; spiculae 2–20 flosculis; lemmata 3-nervia, villosa, aristata, emarginata vel lobata; stamina 1–3 flava; chromosomata: $x = 7$ vel 8.

TYPUS: *Munroa* Torr.

DESCRIPTIONS FOR RECOGNIZED SUBTRIBES

Eleusininae

Plants hermaphroditic. Ligule a membrane or a ciliate membrane. Leaf blades linear. Primary branches of the inflorescence digitate. Spikelets 4–6 mm long; laterally compressed. First glume 1-nerved. Second glume shorter than lower lemma; 1–3(–5)-nerved. Rachilla pronounced between the florets. Florets 3–15 per spikelet. Sterile florets present. Lemma entire; awned, mucronate, or unawned; glabrous; 3–5-nerved; membranous. Palea membranous. Lodicules truncate or acuminate. Fruit with a free pericarp. Base chromosome number, $x = 9, 10$, or 12.

Genera Included: *Dactyloctenium* Willd., and *Eleusine* Gaertn.

Eragrostidinae

Plants hermaphroditic, dioecious, or monoecious. Ligule a membrane, a ciliate membrane, or a line of hairs. Leaf blades filiform, linear, or triangular. Primary branches of the inflorescence not digitate. Spikelets 1–40 mm long; laterally compressed or terete. First glume 1–5-nerved. Second glume shorter than or about the same length as the lower lemma; 1–9-nerved. Rachilla pronounced between the florets. Florets 2–60 per spikelet. Sterile florets present (occ. absent in *Eragrostis*). Lemma entire, emarginate, lobed, or cleft; awned, mucronate, or unawned; glabrous or hairy; 3–9-nerved; hyaline, membranous, chartaceous, coriaceous, or indurate. Palea hyaline, membranous, or chartaceous. Lodicules truncate, rounded, or acuminate. Fruit with an adnate pericarp. Base chromosome number, $x = 10, 20$, or 30.

Genera Included: *Eragrostis* Wolf, *Gouinia* Benth., *Leptochloa* P. Beauv., *Neeragrostis* Bush, *Neesiochloa* Pilger, *Neyraudia* Hook. f., *Redfieldia* Vasey, *Scleropogon* Phil., *Sobnsia* Airy-Shaw, *Steirachne* Ekman, *Trichoneura* Anderss., *Tridens* Roem. & Schult., *Triplasis* P. Beauv., *Tripogon* Roem. & Schult., and *Vaseyochloa* Hitchc.

Monanthochloinae

Plants hermaphroditic or dioecious. Ligule a membrane, a ciliate membrane, or a line of hairs. Leaf blades linear. Primary branches of the inflorescence not digitate. Spikelets 5–30 mm long; laterally compressed or terete. First glume 0–8-nerved. Second glume shorter than or about the same length as the lower lemma; 1–11-nerved. Rachilla pronounced or not pronounced between the florets. Florets 2–25 per spikelet. Sterile florets

present. Lemma entire; unawned; glabrous or hairy; 3–13-nerved; chartaceous, or coriaceous, or indurate. Palea membranous, chartaceous, coriaceous, or indurate. Lodicules truncate or cuneate. Fruit with an adnate pericarp. Base chromosome number, $x = 10, 19$, or 20 .

Genera Included: *Allolepis* Soderstr. & Deck., *Distichlis* Raf., *Jouvea* Fourn., *Monanthochloë* Engelm., *Reederochloa*, and *Swallenia* Soderstr. & Deck.

Muhlenbergiinae

Plants hermaphroditic or andromonecious. Ligule a membrane or a ciliate membrane. Leaf blades filiform or linear. Primary branches of the inflorescence not digitate. Spikelets 0.5–8 mm long; laterally compressed, terete, or dorsiventrally compressed. First glume 1–3-nerved. Second glume shorter than, about the same length as, or longer than lower lemma; 1–4-nerved. Rachilla pronounced or not pronounced between the florets. Florets 1–3 per spikelet. Sterile florets present or absent. Lemma entire, emarginate, or lobed; awned, mucronate, or unawned; glabrous or hairy; 3-nerved; hyaline, membranous, or chartaceous. Palea hyaline, membranous, or chartaceous. Lodicules truncate. Fruit with an adnate pericarp. Base chromosome number, $x = 8$, or 10 . Genera Included: *Bealia* Scribn., *Blepharoneuron* Nash, *Chaboissaea* Fourn., *Lycurus* Kunth, *Muhlenbergia* Scribn., and *Pereilema* Presl.

Munroinae

Plants hermaphroditic, monoecious, or gynomonoecious. Ligule a ciliate membrane, a line of hairs, or absent. Leaf blades linear, or triangular. Primary branches of the inflorescence not digitate. Spikelets 5–12 mm long; laterally compressed. First glume 1-nerved. Second glume shorter than lower lemma, about the same length as the lower lemma, or longer than lower lemma; 1-nerved. Rachilla pronounced between the florets. Florets 2–12 per spikelet. Sterile florets present. Lemma emarginate, lobed, or cleft; awned; hairy; 3-nerved; membranous, or coriaceous. Palea membranous. Lodicules truncate, or cuneate. Fruit with an adnate pericarp. Base chromosome number, $x = 7$, or 8 .

Genera Included: *Blepharidachne* Hack., *Dasyochloa* Rydb., *Erioneuron* Nash, and *Munroa* Torr.

Sporobolinae

Plants hermaphroditic. Ligule a line of hairs. Leaf blades filiform, or linear. Primary branches of the inflorescence not digitate. Spikelets 1–10 mm long; laterally compressed or terete. First glume nerveless or 1-nerved. Second glume about the same length as the lower lemma; 1-nerved. Rachilla not pronounced between the florets. Florets 1 per spikelet. Sterile florets absent. Lemma entire; unawned; glabrous or hairy; 1-nerved; hyaline, mem-

branous, or chartaceous. Palea hyaline, membranous, or chartaceous. Lodicles truncate. Fruit with a free pericarp. Base chromosome number, $x = 8$, 9, or 10.

Genera Included: *Calamovilfa* (A. Gray) Scribn., *Crypsis* Ait., and *Sporobolus* R. Br.

Uniolinae

Plants hermaphroditic. Ligule a line of hairs. Leaf blades linear. Primary branches of the inflorescence not digitate. Spikelets 3–30 mm long laterally compressed. First glume 1–5-nerved. Second glume shorter than lower lemma; 1–5-nerved. Rachilla pronounced between the florets. Florets 5–20 per spikelet. Sterile florets present. Lemma entire; unawned; glabrous; 3–9-nerved; membranous or coriaceous. Palea membranous or chartaceous. Lodicles truncate. Fruit with a free pericarp. Base chromosome number, $x = 10$.

Genera Included: *Tetrachne* Nees and *Uniola* L.

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